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Bionomics, Evolution, and Zoogeography of Members of the Genus *Dicheirus*

(Coleoptera: Carabidae)

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The genus *Dicheirus* contains 6 species and subspecies: *D. brunneus* (Dejean), *D. dilatatus dilatatus* (Dejean), *D. dilatatus angularatus* Casey, *D. obtusus* LeConte, *D. piceus* (Menetries), *D. strenuus* (Horn) (Noonan, 1968). Evolution of the genus, with examination of other genera of the subtribe Anisodactylina are given by Noonan (1973, 1974). The present paper provides a detailed analysis of the evolutionary and zoogeographic relationships of the members of *Dicheirus* and includes additional bionomic information for some species.

BIONOMICS

The following statements are based on field observations of adults primarily in northern and central California but also in southern California, Oregon, and British Columbia.

Members of *Dicheirus* are adapted to grassy habitats lacking trees or with scattered trees such as in woodlands or along grassy forest edges. On rare occasions *D. dilatatus dilatatus* and *D. piceus* occur in moderately moist and possibly slightly brackish grassy areas near ocean bays.

Species occurring in forest climax areas inhabit natural clearings inside forests, the grassy edges of forests, and in man-made clearings. The clearing of forests to create pastures provides additional habitats for such species, and adults are more numerous in pastures than in many natural clearings. Pastures are probably more favorable habitats than many natural clearings due to: discontinuity and small size of many natural clearings; unfavorable factors (such as flooding in clearings formed by streams) present in many natural clearings; and additional

shelter in pastures such as dried cow droppings, fallen fence posts and other debris. Dried cow droppings are especially beneficial to adults; pastures with them contain more individuals than similar areas without. The ground beneath dried cow droppings is often moister and cooler than that adjacent to them, and adults aggregate in these moister, cooler microhabitats.

In central and northern California, teneral adults appear from January to March and are active with adults from the previous year until the ground and vegetation dry during late April to June. Except for isolated lowland areas and mountainous areas in which the ground and vegetation dry later in the year or remain moist, adults are uncommon from approximately June to September. In September or October teneral adults appear, soon mature, and are active with previously matured adults.

In central and northern California an early activity period of adults coincides with winter rains, is reduced during the dry summer, and is renewed prior to and probably also during fall rains. Rainfall is the major factor influencing adult activity. During exceptionally dry years adults of *D. strenuus* and *D. dilatatus dilatatus* do not appear in the fall, and adults of *D. piceus* are greatly reduced in number. Additional field studies may reveal that adults of other forms also do not appear or are reduced in numbers in the fall of dry years.

Specimens of *Dicheirus* have not been observed flying. However, all species but *D. strenuus* have full and apparently functional hind wings. The winged species may have diurnal spring dispersal flights. I have noted in the spring while collecting in very small natural clearings that on warm days adults suddenly appear in areas that had been intensively examined (debris and top 3 or 4 inches of soil removed) just previously. Darlington (1943) suggested that flight is advantageous to species of Carabidae which inhabit relatively large areas with sparse unstable populations. Before the forest clearing activities of man, species of *Dicheirus* presumably were restricted to natural clearings in forest climax areas. Such clearings would have been sparsely distributed, and often small and unstable. Full-winged species probably remained so because of the importance of flight as a dispersal mechanism. The lack of flight records for *Dicheirus* may be due to flight being diurnal and restricted to early spring. Most Carabid flight records are based on captures at lights; if *Dicheirus* adults fly only during the day, then they will not aggregate at lights. Furthermore most insect collectors probably do not begin field work until after early spring.

TABLE 1. Plesiomorphic and apomorphic character states used in Fig. 1.

No.	Character	Character State	
		plesiomorphic	apomorphic
Thorax			
1	pronotal pubescence	moderate to dense throughout	glabrous to sparse medially
2	proepisternal punctures	absent or very small	large and prominent
Legs			
3	venter of articles 1 to 4 of ♂ foretarsi	with spongy pubescent vestiture	glabrous in most specimens, partial to complete spongy pubescent vestiture in some specimens
4	mid and hind tibia	without prominent tubercles at base of spines along sides	with prominent tubercles at base of spines along sides
5	♀ hindtibial apical spurs	lanceolate shaped	slightly laterally expanded a) spatulate shaped
Elytra			
6	pubescence length	short	varied from short to long a) long in all specimens
7	type of pubescence	adpressed	erect
Male genitalia			
8	median lobe	not twisted	twisted

Most forms of *Dicheirus* occur not only in the same geographic area (Figs. 2–6) but, at least in the adult stage, in the same microhabitat. In California I have taken adults together in the same hole beneath debris on the ground as follows: *D. brunneus*, *D. dilatatus dilatatus*, and *D. piceus* in Trinity County; and *D. strenuus* and *D. piceus* in Kern and Tulare Counties. Additional collecting will probably demonstrate that adults of all sympatric forms occur in the same microhabitats.

EVOLUTION

The principles used in evolutionary reconstructions are slightly modified from those of Hennig (1966) as discussed in detail in Noonan (1973). Figure 1 and Table 1 present the most probable hypothesis of evolution of the species and subspecies. All sister taxa in Figure 1 are linked by synapomorphies. Convergence in a character state has occurred once; all specimens of *D. dilatatus angulatus* and some specimens of *D. brunneus* have long elytral setae. A sequence of evolution other than that postulated in Figure 1 and Table 1 would not be consistent with available data.

CONTEMPORARY ZOOGEOGRAPHY

Species are restricted (Figs. 2–6) to western North America, probably due to limited adaptation to continental climate. Eastern limits are represented by specimens of *D. piceus* from Salt Lake County, Utah. Northern and southern limits are set by *D. piceus* in southern British Columbia and on Guadalupe Island off the western coast of Baja California. Guadalupe Island has a persistent summer fog belt in the summit section (Axelrod, 1967) and a milder, moister climate than the immediately adjacent mainland (Savage, 1967). These climatic factors probably explain survival of *D. piceus* on Guadalupe Island, approximately 220 miles farther south than mainland records of *D. dilatatus angulatus* in northwestern Baja California. *Dicheirus dilatatus dilatatus* and *D. piceus* occur on Santa Catalina and San Clemente Islands with *D. piceus* also present on Guadalupe Island. Distances of these islands from the mainland are (Philbrick, 1967) 20, 49 and 157 miles respectively.

Table 2 lists range extents (the linear distance between the 2 most distant occurrences of each form) of the 6 species and subspecies of *Dicheirus*. Previous workers such as Ball and Freitag (1969), Erwin (1970), Noonan (1973), and Whitehead (1972) used range extents to elucidate refugia, and centers of evolution, and to discuss probable adaptability of wide ranging versus narrow ranging forms. The small number of forms in *Dicheirus* and sympatry of most of them make it impossible to stipulate a present center of evolution other than the area now occupied by these forms.

The relatively large range extents of *D. piceus*, *D. obtusus* and *D. dilatatus* suggest that these 3 species are more tolerant than other forms to environmental extremes. Only *D. piceus* and *D. dilatatus dilatatus* show a possible tolerance to brackish habitats near ocean bays and are

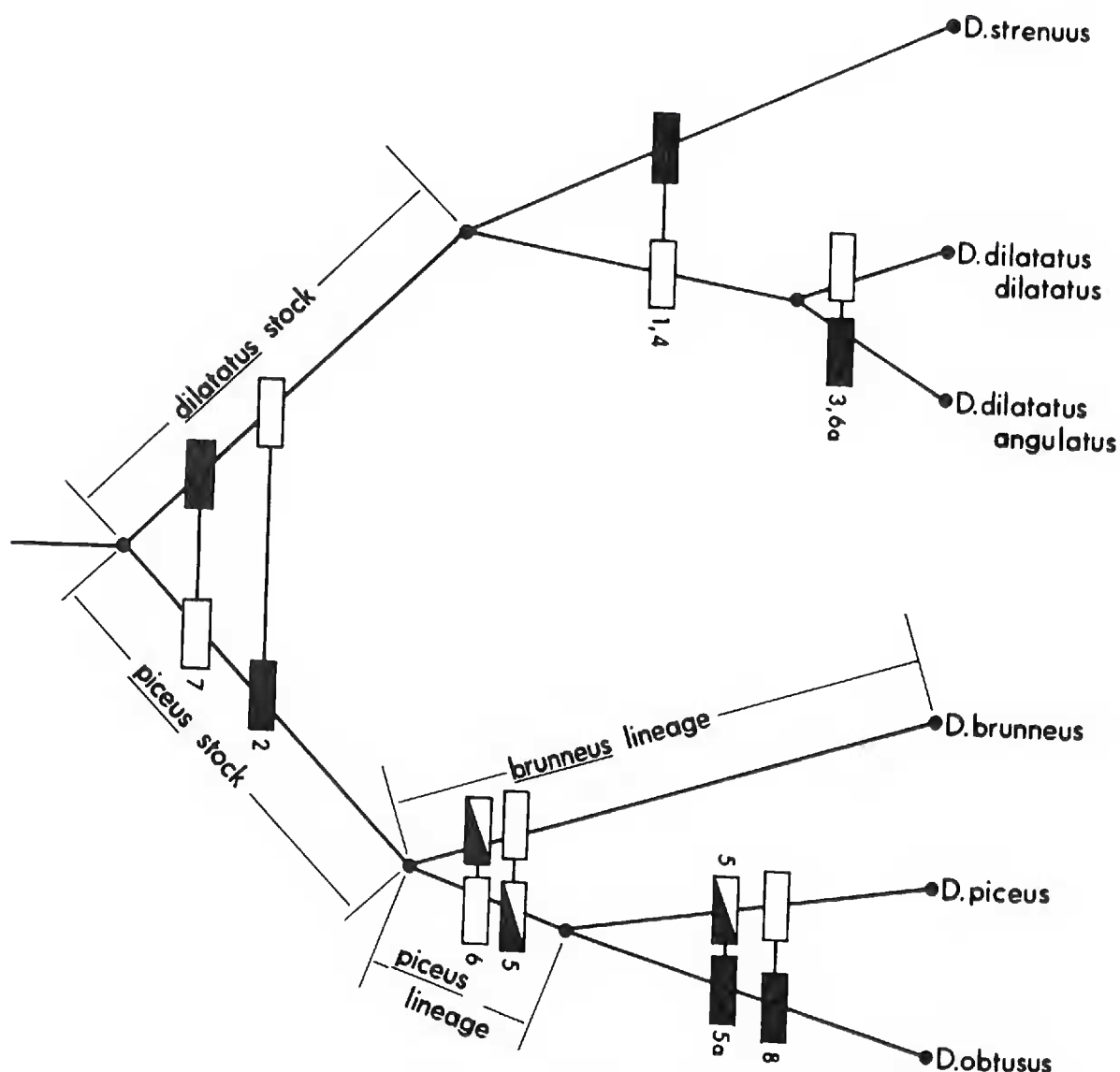


FIG. 1. Postulated evolution of species and subspecies of *Dicheirus* (hollow rectangles denote plesiomorphic character states, half black rectangles denote intermediate apomorphic character states, fully black rectangles denote apomorphic character states).

also the only forms recorded from islands. *Dicheirus piceus* also exists in habitats from which other forms seem excluded.

Dicheirus brunneus has a 450 mile range extent and is apparently adapted only to mesic environmental conditions in northern California and Oregon.

Dicheirus strenuus and *D. dilatatus angulatus* have restricted range extents of 73 and 30 miles respectively. *Dicheirus strenuus* is the only taxon with vestigial hind wings; this condition probably explains in part its restricted range from the Tehachapi and Greenhorn Ranges, Kern and Tulare Counties, California. This species may be adapted to only a narrow range of environmental conditions since it does not follow woodlands or grasslands down into the San Joaquin Valley or high up into the Sierras as do all other forms present in central California.

TABLE 2. Range extents of species of *Dicheirus*.

Species or Subspecies	Maximum Range Extent (in miles)
<i>D. piceus</i>	1700 (Guadalupe Island included) 1200 (mainland only)
<i>D. obtusus</i>	800
<i>D. dilatatus</i> (both subspecies)	750
<i>D. dilatatus dilatatus</i>	650
<i>D. dilatatus angulatus</i>	30
<i>D. brunneus</i>	450
<i>D. strenuus</i>	73

Possibly, *D. strenuus* evolved in its present restricted range. Alternatively, it may formerly have been more widespread, and its low dispersal ability may have resulted in its elimination from much of its range during Pliocene and Pleistocene climatic changes.

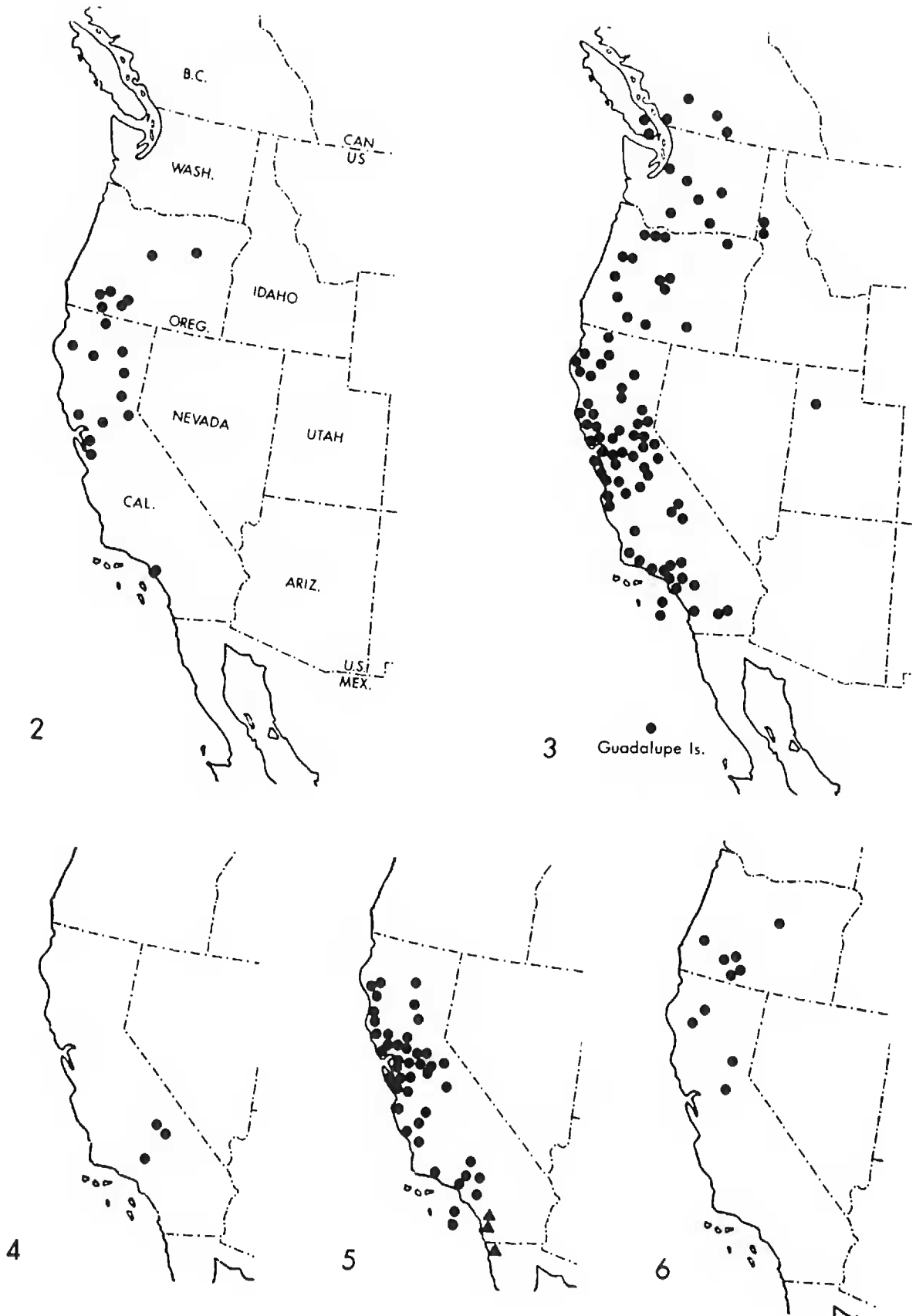
Dicheirus dilatatus angulatus is known only from coastal areas in San Diego County, California and northern Baja California. The factors responsible for such a restricted range are unknown. Possibly *D. d. angulatus* occurs further south in Baja California, but has not been collected.

HISTORICAL ZOOGEOGRAPHY

Taxa of *Dicheirus* demonstrate considerable sympatry (Figs. 2–6), and adults of several species share microhabitats in central and northern California. This sympatry and ecological similarity suggest that extant species have existed long enough to acquire isolating mechanisms enabling them to share the same geographical ranges and, at least as adults, the same microhabitats. The general lack of orderly patterns of vicariance suggest that species may have evolved elsewhere than their present ranges.

Species of *Dicheirus* are now concentrated from approximately southern California to Oregon, but initial evolution within the genus probably occurred in Alaska and northern Canada (Noonan, 1973). According to these ideas, the ancestor of *Dicheirus* crossed from Eurasia into North America via the Bering Land Bridge during the early Tertiary, probably during Eocene when the Bering Land Bridge was present (Hopkins, 1967), and the climate there was temperate (Dorf, 1960).

Eocene tropical and subtropical climates in the United States (Dorf, 1960) may have prevented initial dispersal southward. However, as



FIGS. 2-6. Distribution of: (2) *D. obtusus*; (3) *D. piceus*; (4) *D. strenuus*; (5) *D. dilatatus dilatatus* (circles) and *D. dilatatus angulatus* (triangles); (6) *D. brunneus*.

climates cooled during Oligocene, Miocene and especially Pliocene, there were probably dispersals south into the area now occupied by species of *Dicheirus*. As climates continued to cool, *Dicheirus* became extinct in northern Canada and Alaska. The present irregular and mostly sympatric distribution of species is thus probably due to relatively old species being forced south from their center of evolution.

Eastward dispersal of *Dicheirus* was probably prevented by intolerance of continental climates and to a lesser extent by the Brooks Range and Rocky Mountains. The restrictive climatic factor may have been the past and present seasonal distribution of precipitation. Along the Pacific Coast precipitation is concentrated in winter, and severe drought regularly coincides with summer heat; inland there is a strong summer maximum of precipitation (Wells, 1970). This difference in climatic rhythm may also be the reason why many carabid species of interior grasslands (such as those of the subgenus *Glanodes*, genus *Harpalus*, see Ball, 1972) have not extended their ranges to the Pacific Coast.

The sympatric *dilatatus* and *piceus* stocks probably evolved during Eocene to Miocene north of the present range of *Dicheirus*. *Dicheirus strenuus* and *D. dilatatus* may be vicariant in that *D. dilatatus* is not recorded from the range of *D. strenuus*. However, *D. dilatatus* surrounds the range of *D. strenuus* on the north, south and west. I know of no past or present barriers between the known species ranges; additional collecting will probably establish sympatry.

Dicheirus dilatatus dilatatus and *D. dilatatus angulatus* are separated by a gap of approximately 100 miles in southern California (Fig. 5). Evolution of these subspecies is probably due to the coast corridor effect described by Peabody and Savage (1958) for amphibians and reptiles. During Pliocene and early Pleistocene (Fig. 7) the San Joaquin Valley consisted of a flooded embayment opening to the ocean by a wide strait in northern Baja California. Populations of *D. dilatatus* were probably isolated east of the embayment and evolved into *D. dilatatus angulatus* which has several apomorphies suggesting selection was acting on a small gene pool. Populations west of the San Joaquin embayment probably exchanged genes northward via the coast corridor with other populations and were thus part of a relatively large gene pool. These populations retained plesiomorphic features; their descendants constitute the nominate subspecies with relatively plesiomorphic features. This postulate, that the subspecies with apomorphic features was derived from a smaller gene pool than the sub-

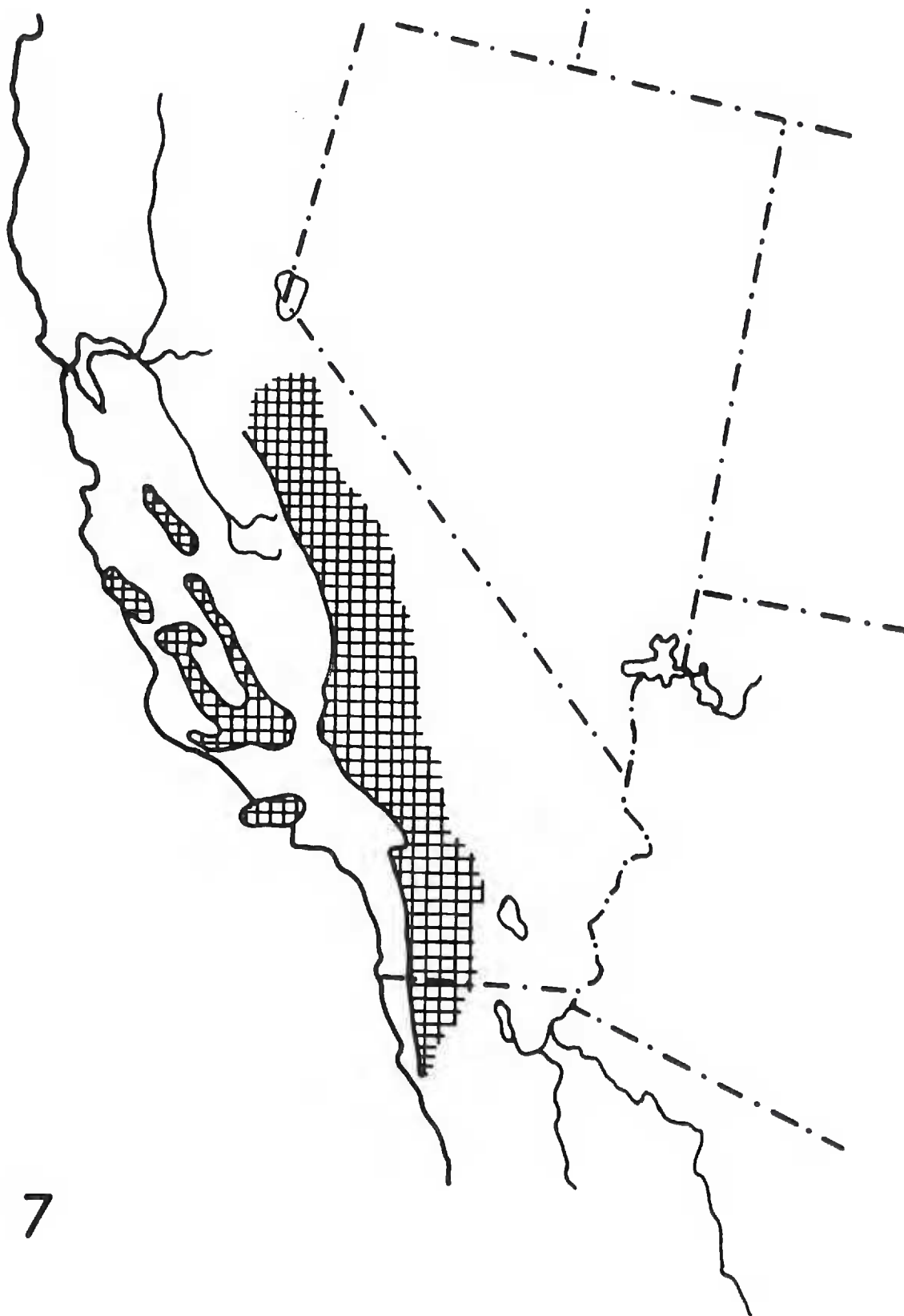


FIG. 7. Pliocene and early Pleistocene paleogeography of California, showing archipelagic nature of Coast Range region, and presence of strait connecting Pacific with San Joaquin embayment. Cross hatching indicates flooded areas. (Adapted from Peabody and Savage, 1958.)

species with plesiomorphic ones, agrees well with Brundin's (1972) description of speciation by cleavage.

As the San Joaquin embayment dried, the climate of eastern southern California probably became drier and warmer; populations of *D. dilatatus angulatus* probably migrated westward toward cooler, moister coastal regions. The Xerothermic Period which lasted from 8,000 to 3,000 years ago constituted a time of warm climate (Axelrod, 1967) which placed particular stress on organisms along the Pacific Coast where precipitation is concentrated in the winter and severe drought regularly coincides with summer heat (Wells, 1970). Any populations of *D. dilatatus angulatus* which remained in eastern southern California after drying of the San Joaquin embayment probably were eliminated by stresses of the Xerothermic. The presence of *D. dilatatus dilatatus* on San Clemente and Santa Catalina Islands and the absence there of *D. dilatatus angulatus* supports the above hypothesis of evolution and dispersal. If *D. dilatatus angulatus* had been present along the coast during the Pliocene and early Pleistocene, it probably would have migrated to these 2 islands as did the nominate subspecies.

Species in Carabid genera other than *Dicheirus* may also have cleaved into subspecies or sister species due to the coast corridor effect. *Calathus ruficollis* Dejean has a distribution similar to that of the genus *Dicheirus* and is found in habitats similar to those of *Dicheirus* (Ball and Nègre, 1972). The coast corridor effect probably explains the differentiation of *C. ruficollis ignicollis* Casey from the nominate subspecies.

If the 2 subspecies of *D. dilatatus* evolved as a result of the San Joaquin embayment, then they have had approximately 2 million years since its disappearance in which to become parapatric. All apomorphic character states of *D. dilatatus angulatus* but long elytral setae vary toward the plesiomorphic state found in the nominate subspecies, and some individuals have the plesiomorphic state for one or more characters. This variation suggests that the 2 subspecies were parapatric in the past and had limited gene exchange. Such parapatry probably took place during cooler, moister (Axelrod, 1967) Pleistocene glacial periods.

My impression of the area now separating the 2 forms (Fig. 7) is that it does not have favorable habitats for *Dicheirus*; *D. piceus*, the most widespread species in the genus, is absent from this area but is found both to the south and north. Mainland records of *D. dilatatus dilatatus* north of the Tehachapi Mountains are mostly based on moderate to extensive series of specimens; records south of these mountains are mostly based on only a few specimens per locality. This apparent reduction in

abundance south of the Tehachapi Mountains suggests that this subspecies is not well adapted to conditions in southern California. Finally *D. dilatatus angulatus* survives only in a small refugium along the coast from San Diego County, California to northern Baja California. Increasing warmth and aridity after Pleistocene glacial periods (Axelrod, 1967) probably eliminated all *Dicheirus* from the present gap between the subspecies of *D. dilatatus*.

Rates of differentiation in *D. dilatatus* can be estimated from geological dating of the San Joaquin embayment which existed from approximately 8 to 2 million years ago (dates personal communication from R. Fox). Thus, the subspecies are a maximum of 7 million years old and took 6 million or less years in which to evolve.

Whitehead (1972) calculated the period of time required for speciation in *Schizogenius* and *Brachius* by estimating the age of each group and then counting the number of bifurcations in the reconstructed phylogenies. Such calculations are prone to error both from mistakes in the estimated ages of groups and from errors in the reconstructed phylogenies which most often are simplifications of complex processes which occurred in nature (Noonan, 1973). When fossils are not available, the most reliable estimates of time required for speciation or subspeciation are those based on geologic dating of barriers which isolate or once isolated vicariant sister forms.

Whitehead calculated the average time required for speciation in North American *Schizogenius* and *Brachinus* carabids to be approximately 3 million years. Geological dating of the San Joaquin embayment is not exact; the period of isolation of populations of *D. dilatatus* may have been less than 6 million years, but certainly not less than 3 million.

The *brunneus* and *piceus* lineages are sympatric as are the species *D. brunneus*, *D. piceus* and *D. obtusus*; little can be concluded other than that these taxa probably evolved during the Eocene to Pliocene north of the present range of *Dicheirus*.

Present Utah populations of *D. piceus* are separated from the main species range by nearly 300 miles of Great Basin Desert. Precipitation in lower elevations of this desert is less than 4 inches per year while January/July temperatures average 44.5°/86°F at Las Vegas, Nevada, 32.5°/71°F at Reno, Nevada, and 30°/77°F at Salt Lake City, Utah (Morrison, 1965). This dry and moderately warm climate probably bars dispersal between the main range and the Utah populations, presumably localized in mountains east of Salt Lake City. However, Miocene and Pliocene climates of the Great Basin were subhumid with 25 to 30 inches per year of estimated precipitation, and the present desert

climate did not begin until early Pleistocene (Morrison, 1965). Pleistocene glacial periods resulted in temperatures 8° to 15° F cooler than now, more rainfall, and shifts of life zones hundreds of miles north and south and thousands of feet up and down mountains. Before Pleistocene development of desert climate and during Pleistocene cool, moist periods, populations of *D. piceus* probably invaded the Great Basin Deserts and reached Utah. The desert climate of the present and of the interglacial periods probably eliminated *Dicheirus* from Great Basin lowlands and isolated populations of *D. piceus* in mountains presently moister and cooler than lowlands.

An alternative explanation for the presence of isolated populations of *D. piceus* in Utah is as follows. Before the development of desert climate and/or during Pleistocene glacial periods, populations of *D. piceus* (and possibly other species of the genus) may have dispersed around the northern periphery of the Great Basin Desert and then south into Utah via foothills of the Rockies. However, such dispersal would require greater tolerance to continental climate than now shown by species of *Dicheirus* and probably would have resulted in isolated populations of *D. piceus* in Montana, Wyoming, and Colorado. Collecting has not demonstrated the existence of such populations; dispersal directly across the Great Basin Desert seems more probable than dispersal along the northern periphery and Rockies.

The effects of Quaternary glacial periods on western North America are not as well elucidated as for the East. However, various workers (Crandell, 1965; Martin and Mehringer, 1965; Morrison, 1965; Wahrhaftig and Birman, 1965) agree that temperatures were cooler, precipitation greater, and that biotic zones shifted downward. Such climatic changes may have resulted in migrations south into Baja California. Continental climates probably prevented migrations southeast into mainland Mexico. If migrations had reached mainland Mexico, relict populations of *Dicheirus* would probably occur in the highlands as do other members of the subtribe Anisodactylina (Noonan, 1973).

The presence of *D. dilatatus dilatatus* and *D. piceus* on Santa Catalina and San Clemente Islands and of *D. piceus* on Guadalupe Island may be due to dispersal across present water gaps by wind or by rafting. Dispersal to the first 2 islands could not have been earlier than their formation during or after the mid-Pliocene (Valentine and Lipps, 1967). Ocean barriers between the mainland and these 2 islands were absent (Clements, 1955, as reported by Valentine and Lipps, 1967) or at least much narrower during late Pliocene and early Pleistocene (Valentine and Lipps, 1967). Colonization probably took place then. Migration

onto other Channel Islands may also have occurred at that time. The lack of records of *Dicheirus* from other California Channel Islands may be due to lack of collecting or to chance extinction.

Guadalupe Island possibly was never connected to the mainland (Garth, 1967), and *D. piceus* probably colonized it by long distance dispersal over water. However, geological data regarding mainland connections of Guadalupe are somewhat inconclusive, and colonization via a land bridge remains a possibility.

The above discussion illustrates that species of *Dicheirus* are mostly sympatric and probably evolved north of their present ranges. It also demonstrates the difficulty of elucidating place or time of origin of forms which do not exhibit vicariance or have a fossil record.

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RECENT LITERATURE

THE CIID BEETLES OF CALIFORNIA (COLEOPTERA : CIIDAE). John F. Lawrence. *Bulletin of the California Insect Survey*. Volume 17, 41 pp., 7 figs., 15 maps. \$2.25.

This summary of the biology, systematics and geographic distribution of the California representatives of an abundant but little-noticed family of fungus-inhabiting beetles could well be used as a model for similar faunal surveys. The systematics section is prefaced by concise but informative discussions of bionomics, host and habitat preference, seasonal occurrence, and patterns of geographic distribution, and supplemented by tables summarizing information that would have required many pages if presented as raw data. The taxonomic treatment includes introductory explanations of important characters, as well as brief differentiations from similar beetles which occur in bracket fungi and might be confused with Ciidae. The excellent keys to genera and species utilize features which mostly show clear, qualitative differences. Difficult characters are quantified, especially in keys to species. Maps showing characteristic types of distributions are provided for about one half the species. All maps have insets depicting the entire North American distribution, a very helpful addition which requires no additional space. The 37 figures include line drawings of most of the important taxonomic characters, and excellent half tone illustrations of 14 of the 27 species known or suspected to occur within the political boundaries of California.

A comprehensive summary of this nature might well alert ecologists to the opportunities these beetles offer for studies of competition, habitat preference and partitioning or species diversity and niche breadth.—*Editor*.